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EFFECT OF CLEARCUTTING ON ARTIFICIAL EGG PREDATION IN BOREAL
MIXEDWOOD FORESTS IN NORTH-CENTRAL ALBERTA

by

SUSAN ELIZABETH COTTERILL



A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfilment of the requirements for the degree of Master of Science

Department of Zoology

Edmonton, Alberta

Spring 1996



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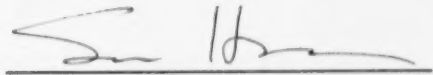
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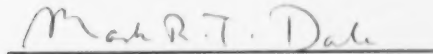
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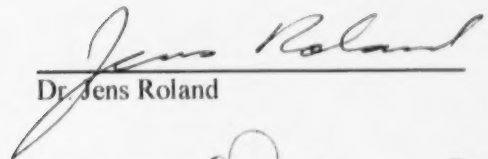
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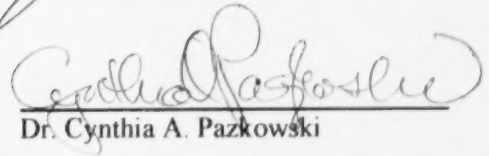
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ABSTRACT

Effect of clearcutting on the rate of artificial egg predation and egg predators was examined in Alberta's boreal mixedwood ecoregion in 1993 and 1994. Control sites remained unfragmented for the two year study. Treatment sites were isolated by clearcutting following the 1993 field season. Plasticine eggs and nest cameras were used to identify predators; and corvids, potential egg predators, were censused. Effect of nest site and landscape attributes on the probability of egg predation was also examined.

Clearcutting did not affect the rate of egg predation or corvid densities, nor did the rate of egg predation vary with distance into aspen forest from a clearcut edge. Predation levels increased significantly in 1994 in both continuous and fragmented sites. Deer Mice (*Peromyscus maniculatus*) and Red Squirrels (*Tamiasciurus hudsonicus*) were the primary predators of ground nests and shrub nests, respectively. Probability of egg predation by Deer Mice and Red Squirrels could not be accurately predicted based on nest site vegetation or landscape characteristics.

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CHAPTER 1. THESIS INTRODUCTION

Habitat fragmentation occurs when portions of the original landscape are removed or altered, creating isolated remnants surrounded by a matrix which differs from the original habitat in structure and microclimate (Whitcomb *et al.*, 1981; Wilcove *et al.*, 1986). Alteration and degradation of habitat are associated with declines of many wildlife and plant species (see Wilcove *et al.*, 1986). In North America, research efforts have focused heavily on declines of neotropical migratory songbirds breeding in eastern deciduous forests (Gates and Gysel, 1978; Whitcomb *et al.*, 1981; Ambuel and Temple, 1983; Robbins *et al.*, 1989). Several mechanisms have been proposed to explain these declines: 1) decreased reproductive success caused by loss and fragmentation of breeding habitat; 2) increased mortality due to habitat loss and fragmentation on wintering grounds; and 3) increased mortality during migration caused by degradation and loss of migratory stopover sites (Böhning-Gaese *et al.*, 1993; Donovan *et al.*, in press).

One of the consequences of habitat fragmentation is the formation of edge at the interface between the two different habitats. Traditionally, creation of forest edge has been favoured by wildlife managers because some species of wildlife, especially game animals, prosper in this transition zone between forest and the adjoining habitat (Leopold, 1933; Wilcove *et al.*, 1986; Hunter, 1990). Bird abundance and diversity have also been observed to increase at forest edges (Strelke and Dickson, 1980; Hansson, 1983; Helle, 1985). Abundant nesting and foraging sites created by higher light intensity, greater foliage density, more foliage layers and a greater abundance of insects

at edges attract birds (Strelke and Dickson, 1980). It has become apparent however, that negative edge effects such as competition, egg predation (Gates and Gysel, 1978; Ambuel and Temple, 1983; Wilcove, 1985) and brood parasitism (Brittingham and Temple, 1983) also exist at forest edges and may have significant adverse impacts on forest avifauna.

Mammalian and avian generalist predators are attracted to edges and may use them as natural travel lanes (Ratti and Reese, 1988). An increased amount of edge allows predators easier access to the forest interior (Langen *et al.*, 1991). These predators can then systematically and efficiently search small fragments of forest, resulting in an elevated rate of egg predation (Martin, 1988). Neotropical migratory species typically raise a single brood, build open nests on or near the ground and have small clutch sizes. These traits may increase their vulnerability to egg predation (Whitcomb *et al.*, 1981). A survey of nest success and mortality for 32 neotropical migratory species revealed that 77% of the total mortality was caused by egg predation (Martin, 1992). Böhning-Gaese *et al.* (1993) suggested that egg predation on breeding grounds in North America had a larger impact on population levels of neotropical migrants than fragmentation of wintering ground habitat.

The boreal mixedwood forest in north-central Alberta is an important breeding habitat for many avian species, particularly many neotropical migrants. Part of the circumpolar boreal forest, the boreal mixedwood covers approximately 49% of the province and is dominated by Trembling Aspen (*Populus tremuloides*) and Balsam Poplar (*Populus balsamifera*) (Strong, 1992). This ecosystem is rapidly being

fragmented by the natural resource industry, including oil and gas exploration and forestry operations. In an effort to diversify Alberta's economic base, logging of aspen and poplar hardwoods by pulp and paper industries began in the fall of 1993. Approximately two-thirds of the boreal mixedwood region in Alberta has been leased by the Alberta government to various forestry companies. Many of these forest companies currently use a two pass clearcutting system. This clearcutting strategy will create small and isolated patches of aspen mixedwood habitat and a tremendous amount of forest-clearcut edge, potentially resulting in negative edge effects, including an increase in egg predation.

While many studies have linked increased egg predation to a decrease in nesting success of songbirds in eastern deciduous forests in North America (e.g. Gates and Gysel, 1978; Whitcomb *et al.*, 1981) and in boreal forests of northern Europe (e.g. Andrén *et al.*, 1985), very few studies examining negative edge effects have been conducted in Canada's boreal forests (Hannon, 1993). Large scale forestry operations underway in Alberta's boreal mixedwood region presented an excellent opportunity to assess effects of clearcutting and negative edge effects, particularly on egg predation.

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CHAPTER 2. CLEARCUTTING DOES NOT AFFECT ARTIFICIAL EGG PREDATION IN BOREAL MIXEDWOOD FORESTS IN NORTH-CENTRAL ALBERTA

INTRODUCTION

Population declines of many migratory songbird species have been attributed in part to fragmentation of tropical and temperate forests (Terborgh, 1989; Böhning-Gaese *et al.*, 1993). In particular, research efforts have focused on declines of neotropical migrants breeding in fragmented eastern deciduous forests of North America (Whitcomb *et al.*, 1981; Wilcove *et al.*, 1986; Robbins *et al.*, 1989). Declines of neotropical migratory songbird populations are not as pronounced in western North America (Sauer and Droege, 1992; Peterjohn and Sauer, 1993). However, this area is being subjected to greater pressure from natural resource extraction and recreational use which may adversely affect ecosystems and wildlife.

Fragmentation often increases the amount of edge or introduces a different type of edge into forested landscapes. Use of edges as natural travel lanes (Bider, 1968) and elevated bird densities at edges (Gates and Gysel, 1978) may attract predators, causing elevated predation rates along edges and into adjacent forest. Egg predation has been implicated as one of the primary factors negatively affecting songbird reproductive success in fragmented landscapes (Gates and Gysel, 1978; Whitcomb *et al.*, 1981; Robinson *et al.*, 1995).

Several artificial egg predation studies identified corvids as primary egg predators in boreal coniferous forests (Angelstam, 1986; Andrén, 1992), aspen dominated hardwood stands (Yahner and Scott, 1988) and in boreal mixedwood stands in Alberta

(Hannon, 1993). Andrén (1992) also documented an increase in corvid density and a change in the corvid species complex as forests became more fragmented. I predicted: 1) that corvids would be important egg predators in my study area; 2) and that following fragmentation, corvids associated with open areas (e.g. American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*) and Black-billed Magpie (*Pica pica*)) would become more common while abundance of forest-living corvids (Common Raven (*Corvus corax*) and Gray Jay (*Perisoreus canadensis*)) would decline.

The majority of studies examining effects of forest fragmentation on egg predation have been conducted in eastern deciduous forests (Wilcove, 1985; Small and Hunter, 1988) and Scandinavian coniferous forests (Andrén and Angelstam, 1988; Möller, 1987; Andrén, 1992; see Andrén, 1995). Although egg predation was studied in forested areas, the surrounding matrix was dominated by agricultural lands in all of these studies. Fewer studies have examined edge effects in landscapes dominated by forest and fragmented by clearcutting (see Andrén, 1995). Andrén (1995) suggested that negative edge effects associated with habitat fragmentation were more pronounced in homogeneous forests and in forests surrounded by farmland. In contrast, heterogeneous forests with many natural edges, and forest dominated landscapes had diminished or no negative edge effects (Ratti and Reese, 1988; Noss, 1991; Rudnicki and Hunter, 1993).

The western boreal forest supports the richest avifauna community in North America, north of Mexico. Neotropical migrants comprise approximately 40% of this community (Smith, 1993). Historically, wildfire and insect outbreaks were the dominant disturbances in the boreal mixedwood while human induced disturbances occurred at

relatively small scales (Stelfox, 1995). However, technological advances have enabled the use of Trembling Aspen (*Populus tremuloides*) and Balsam Poplar (*P. balsamifera*) in pulp and paper production (Peterson and Peterson, 1992). As a result, over two-thirds of the boreal mixedwood have been leased by the provincial government to various forestry companies. Very few studies have examined the impact of forest fragmentation by logging on birds breeding in the boreal mixedwood region in Alberta (Hannon, 1993; Nietfield and Stelfox, 1993).

Aspen dominated mixedwood forests are typically logged using a two pass clearcutting strategy in which alternating aspen patches are removed from across the landscape. This cutting design results in wide-scale fragmentation of the landscape and introduces a tremendous amount of forest-clearcut edge into the forest. Creation of foreign edge may result in an increase in the rate of egg predation which would negatively impact songbirds nesting in this area. Proactive research examining the impact of clearcutting on egg predation is critical as the forest industry expands into this ecoregion in Alberta and across Canada.

I established a pre- and post-logging study to investigate the impact of clearcutting on the rate of egg predation and on the abundance of potential egg predators. An estimate of egg predation was obtained before (1993) and after logging (1994). Egg predation was assessed indirectly using artificial nests and eggs. My specific objectives were as follows: 1) to assess the impact of newly created forest-clearcut edge on the rate of egg predation in remnant forest patches; 2) to determine if distance from a clearcut edge affects the egg predation rate; 3) to examine the effects of clearcutting on species

composition and density of corvids, potential egg predators; 4) to compare predation pressure on ground and shrub nests; 5) to identify the major egg predators; and 6) to determine if nest site vegetation and landscape characteristics influence the probability of a nest being depredated.

METHODS

Study Area

I conducted this research west of Calling Lake, Alberta (55° 15'N, 113° 19'W) in 4 adjacent 10 x 10 km townships. The study site was located within the boreal mixedwood forest (Figure 2-1), an ecoregion dominated by Trembling Aspen and Balsam Poplar. Study sites were located in stands aged 75 years or older. Variation in topography, soil types and stand attributes has resulted in a complex landscape mosaic (Stelfox, 1995). White Spruce (*Picea glauca*) and Balsam Fir (*Abies balsamifera*) are climax species but are present in low amounts due to a frequent natural disturbance regime (Strong, 1992). Jack Pine (*Pinus banksiana*) stands predominate on sandy soils and extensive Black Spruce (*Picea mariana*) stands and wetlands are common throughout the boreal mixedwood ecoregion (Strong, 1992). A variable understory vegetation complex is characterized by Prickly Rose (*Rosa acicularis*), Green Alder (*Alnus crispus*), Low-bush Cranberry (*Viburnum edule*), Wild Sarsaparilla (*Aralia nudicaulis*), Bunchberry (*Cornus canadensis*) and Bracted Honeysuckle (*Lonicera involucrata*).

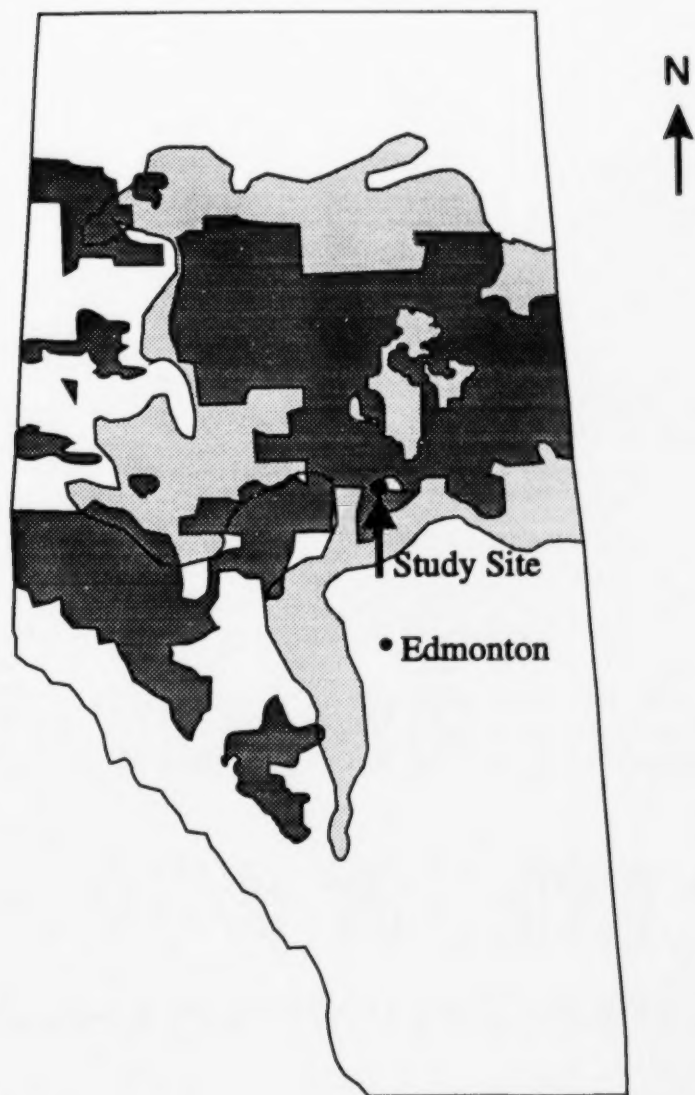
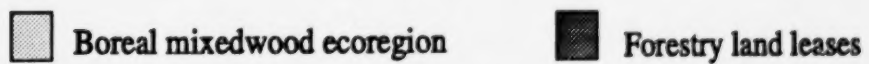


Figure 2-1. Study site location within the boreal mixedwood ecoregion and land leased by forestry companies in Alberta.



Experimental Design

During the summer of 1993, I conducted all research in unfragmented aspen and poplar forests. The treatment township (72-24) was logged by Alberta Pacific Forest Industries Inc. (Al-Pac) in winter of 1993-1994; alternating cutblocks were removed on the first pass of harvest. Remaining second pass cutblocks will be harvested when the regrowth in the clearcuts is 3 m high or at least 10 years have passed. Cutblocks were on average 40 ha in size, irregularly shaped so as to limit the line of sight to 400 m, and the maximum width of a cutblock was 400 m. Single trees and small clumps of trees were left standing on a site-specific basis for conifer understory protection. Tree tops and limbs were spread over the clearcut areas (Alberta Pacific Forest Industries Inc., 1993). Control sites in three other townships (71-23, 72-23 and 73-24) remained unfragmented for the two years of the study. The Calling Lake Fragmentation Project (Schmiegelow and Hannon, 1993) was also located within these townships. Experimental clearcutting for the Fragmentation Project occurred within one control township during autumn 1993. My control sites were located a minimum of 200 m from these clearcut areas. An independent conifer logging company also clearcut a small area of conifer stands within this control township during the winter of 1993-1994.

Based on a one-tailed *a priori* power analysis, a sample size of 11 second pass cutblocks was necessary to detect an effect size of a 20% increase in egg predation rates in fragmented compared to unfragmented forests with a power of 0.80. The effect size was standardized (Cohen, 1969) using data from Yahner and Cypher (1987). The standard deviation ranged from 0.098 to 0.179 for predation rates on artificial nests

placed 1.5 m off the ground within 4 year old clearcuts, 8 year old clearcuts and mature forest in the Yahner and Cypher study (1987). In recognition of the tremendous variability that exists within natural systems, a 20% effect size was selected.

Artificial Egg Predation Experiment

Nineteen nest transects were located within 11 second pass cutblocks. These cutblocks were located within an approximately 25 km² area in a 10 × 10 km township (Figure 2-2). In 1993 these sites were unharvested (temporal controls). In the winter of 1993-1994 surrounding first pass cutblocks were clearcut (treatment) (Figure 2-3). The eight second pass cutblocks greater than 20 ha in area contained two nest transects each, located a minimum of 300 m apart. Three second pass cutblocks with areas less than 20 ha contained 1 nest transect each. An equal number of transects and nests were located in unfragmented control forests (spatial controls). The control nest transects were also a minimum distance of 300 m apart and were grouped into 11 'blocks' or units, with 2 nest transects per block. I excluded one control nest transect from analyses of 1994 data because a conifer cutblock adjacent to the transect was clearcut during the winter of 1993-1994.

I placed artificial nests at 20 m intervals, offset 5 to 30 m from the transect lines, with a minimum of 10 to a maximum of 20 nests per transect, depending on the width of the second pass cutblock. Ground nests alternated with shrub nests along a transect. Transects were marked with flagging tape, while nest locations were not marked. Nest sites were characterized by a site description, compass bearing and distance from the

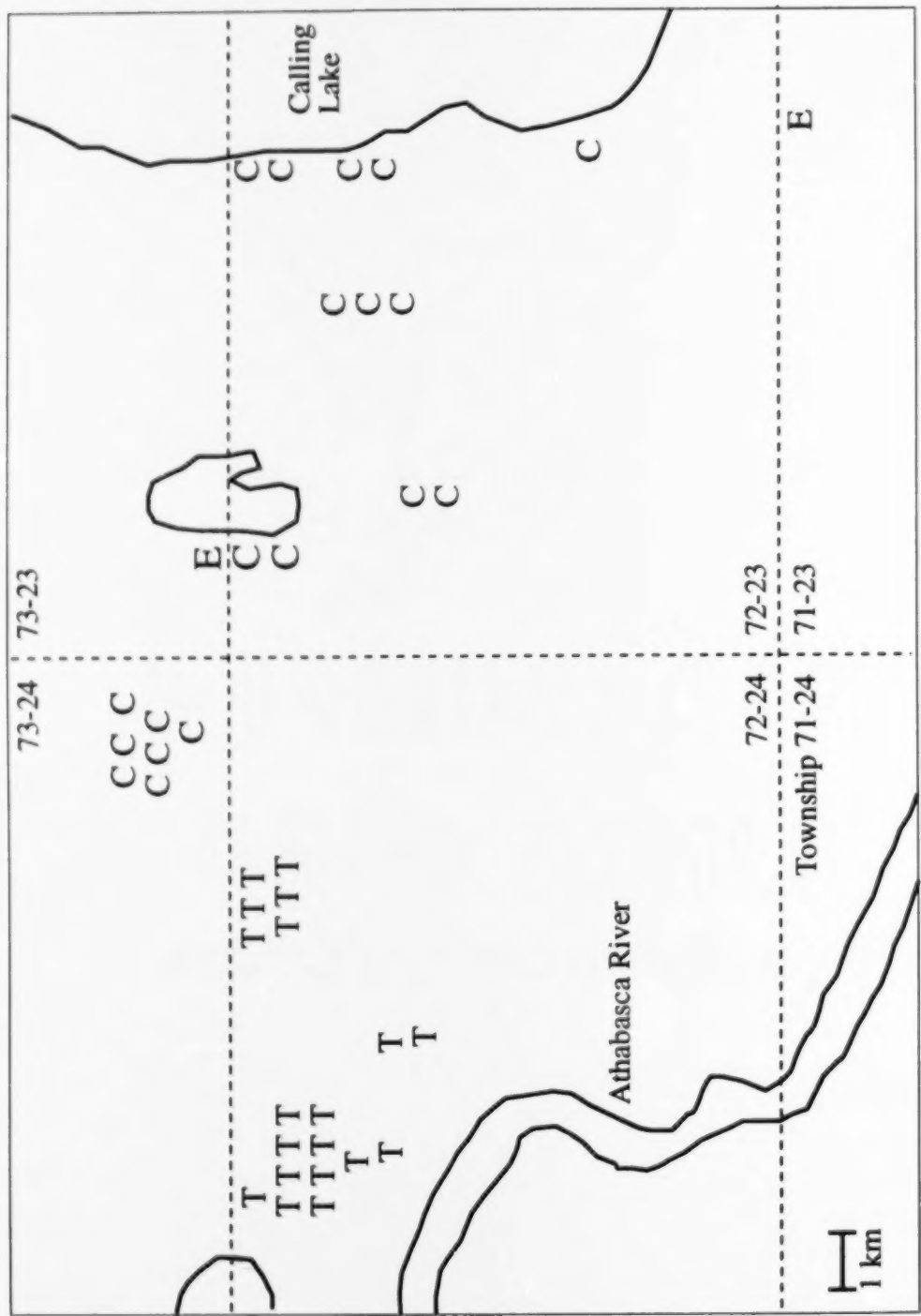
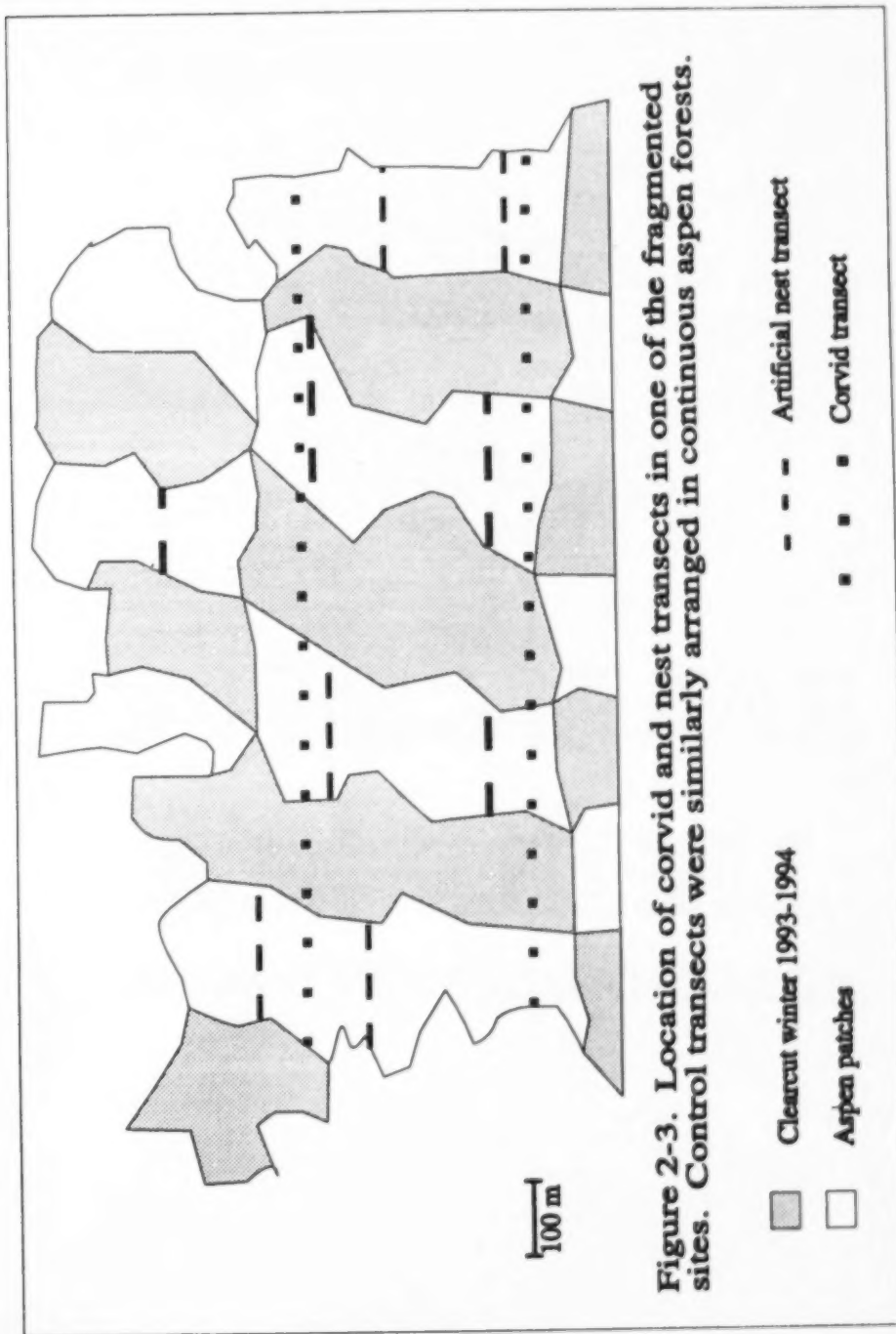


Figure 2-2. Spatial layout of control (C), treatment (T) and edge (E) artificial nest transects.



transect. I placed nests from edge to edge of second pass cutblocks in both 1993 (pre-cut) and 1994 (post-cut). In order to examine predation pressure at distances greater than 200 m from a clearcut edge (maximum width of cutblock = 400 m), I established two additional transects in 1994, that ran 680 m into continuous forest from a clearcut edge. Large aspen stands not slated for clearcutting during the 2 years of my study were difficult to locate. As a result of this difficulty, control sites and the 1994 edge sites were more widely dispersed across the landscape than the treatment sites and were located within an approximately 100 km² area in four 10 × 10 km townships (Figure 2-2).

A total of 555 and 654 nests were used in 1993 and 1994, respectively. Ground nests were set at the base of a tree or log under herbaceous cover with eggs placed over nails marked with small tags of flagging tape to facilitate location of the nest if the eggs were removed. Shrub nests consisted of small wicker aviculture baskets camouflaged with mud and lined with dry grass and leaves. These nests were placed 0.5 m to 2.0 m off the ground, primarily in Green Alder, River Alder (*Alnus tenuifolia*), White Spruce or Balsam Poplar shrubs and saplings. Each nest was baited with a Chinese Painted Quail (*Coturnix chinensis*) egg and a plasticine egg painted to mimic the quail egg. The quail eggs were on average 25 mm in length and 19 mm in width, slightly larger than a Hermit Thrush (*Catharus guttatus*) egg. I used plasticine eggs to aid in predator identification from teeth and beak marks left in the plasticine (Møller, 1987).

I conducted the artificial egg experiment from 30 May to 24 June of 1993 and 1994, coinciding with the egg-laying and nestling period of many of the migratory songbirds found in the study area. Nests were checked once a week for three weeks and

any disturbance or predation event was recorded. To minimize human scent, disposable rubber gloves were worn when setting out eggs and checking nests. Although nests were placed on the same transects in 1994 as used in 1993, ground and shrub nest sites were interchanged and nests were placed in new locations to decrease the possibility of predators memorizing nest locations (e.g. Sonerud *et al.*, 1987).

Nest Cameras

To photograph potential egg predators, I placed cameras at depredated nests and re-baited the nests. The camera system consisted of an artificial nest with a trigger switch electronically connected to an Olympus Infinity Jr. automatic camera (R.M. DeGraaf, pers. comm.). During 1993, 3 cameras were used for a total of 35 camera days. Camera use was intensified in 1994, with the use of 8 cameras for 190 camera days.

Corvid Surveys

I estimated corvid abundance and species composition by conducting surveys along 9 line transects established across control sites and 10 line transects established across treatment sites. Transects were a minimum of 400 m apart and transect length ranged from 1.1 km to 1.6 km. Stations were placed at 200 m intervals along a transect and perpendicular lines extended 100 m on either side of a station (Spytz, 1993). Between 22 and 30 ha were covered during each survey. Observers walked slowly on the transect and out on the 100 m extensions, periodically stopping for several minutes to

listen. All visual and auditory observations of corvids along the transect were mapped. Transects in the treatment township traversed first and second pass cutblocks before and after harvest. Each transect was surveyed 3 times per year, between late May and mid-July, for approximately 2.5 hours per visit.

Vegetation Sampling at Artificial Nest Sites

At each nest site I recorded tree and understory characteristics using the point-quarter technique (Krebs, 1989), following the protocol of Hannon (1993). Trees were classified as having a diameter at breast height (DBH) greater than 8.0 cm; the understory was classified as shrubs and saplings greater than 0.5 m in height with a DBH of less than 8.0 cm. The following measurements were recorded for the nearest shrub or sapling and tree in each quadrant: distance from the quadrant center, species, DBH and number of stems; shrub height was also measured. The 'Quarter Program' (Krebs, 1989) was used to determine tree and shrub density and dominant tree species at the nest site from the point-quarter data. DBH, height and species were recorded for each nest tree or shrub. The percentage of the nest concealed by overhead vegetative cover within an imaginary circle with 0.5 m radius centered on the nest, was estimated by looking down on a ground nest or up from under a shrub nest. The amount of vegetative material covering the nest, viewed at eye level from all sides, was determined to estimate percent lateral cover. Herb height, percent herb cover and percent leaf litter were measured within a 0.3 x 1.0 m quadrat. Based on a visual survey of the immediate nest site area, the quadrat was placed on the most common ground cover surrounding the nest. Canopy

cover directly above the nest was measured using a spherical densiometer and canopy height was measured using a clinometer.

Landscape Attributes

I measured landscape attributes within and around second pass cutblocks (remnant patches) and control 'blocks' using aerial photos taken before and after clearcutting. Although the physical attributes (size, width, shape, area) of second pass cutblocks varied, all control 'blocks' were delineated using a 40 ha (0.4 x 1.0 km) rectangle, based on the maximum width (400 m) and average area (40 ha) of cutblocks as defined by Al-Pac's Timber Harvest Planning & Operating Ground Rules (1993). Landscape features were quantified within three 'buffers' which encircled each cutblock or control block at 250 m, 450 m and 1 km, from the edge of the block. The buffers mimicked the shape of the cutblock or block. These distances represent off-territory foraging and mate searching forays by adults, and juvenile dispersal distances of the three primary egg predators identified in this study: Deer Mouse (*Peromyscus maniculatus*), Red-backed Vole (*Clethrionomus gapperi*) (King, 1968; R. Weaver, unpub. data) and Red Squirrel (*Tamiasciurus hudsonicus*) (Larsen and Boutin, 1994), respectively.

The landscape and block features were quantified using a Placom digital planimeter and 1:15 000 aerial photos. Areas of the following attributes were measured and then standardized to percentages: conifer forest cover, deciduous forest cover, lake/river cover, new clearcut, previous clearcut (approximately 13 years old) and

bog/wetland. Cumulative length of seismic cutlines and roads were measured and presence of open areas greater than 0.45 ha within each block were determined. Length of edge, area and average width of each cutblock and control block were determined and an edge:area ratio was calculated. Percent conifer content for each cutblock/block was estimated by determining the ratio of the number of conifer trees measured, to the total number of trees measured during the point-quarter surveys. Canopy cover for each nest site within a block were averaged to obtain a mean block canopy cover.

Statistical Analyses

I considered a nest to be depredated if either one or both eggs were damaged or missing. Three nests in which two different predators were identified as having damaged the eggs within the same week were not included in the analyses (e.g. plasticine egg - mouse predator; quail egg - unknown: bird or mammal predator). During 1993 and 1994, eggs with minimal amounts of damage were collected from 47 and 8 nests, respectively. Damage was subsequently assessed as being caused by insects or shrews and not considered predation attempts. I did not include these nests in the analyses.

I used SPSS for Windows (SPSS Inc., 1993) for all statistical analyses and set the α level at 0.05 for all statistical tests. Power analysis (Cohen, 1969) was recalculated based on a t-test approximation, using 1993 and 1994 data.

Influence of nest site vegetation on the probability of a nest being depredated was examined using logistic regressions. The following nest site vegetation characteristics were included in the logistical regressions: canopy cover, canopy height, percent herb

cover, average herb height, percent lateral cover at the nest, percent overhead cover at the nest, percent leaf litter, shrub density, tree density, and whether the dominant tree at the nest site was a conifer or not (see Appendix 1). Main effects models were constructed. Logistic regressions were also used to examine the influence of landscape features on the probability of a nest being depredated by mice or Red Squirrels (see Appendices 2 and 3). All variables expressed as percentages were arcsine transformed. Due to the small sample size, only main effects models were constructed.

RESULTS

Predation Pressure on Ground and Shrub Nests

Significantly more ground nests were depredated than shrub nests in both 1993 and 1994 in control and treatment sites (Table 2-1). Mean predation rates on ground nests ranged from a low of 30% in pre-cut sites in 1993 to a high of 85% in control sites in 1994. Mean predation rates on shrub nests ranged from a low of 16% in control sites in 1993 to a high of 45% in control sites in 1994. Ground and shrub nests were subsequently separated for analyses because of the difference in predation pressure and because they represent different nesting guilds. Only in analyses where predation events were grouped by predator type were the nest types combined. Substantial increases in predation pressure on ground nests occurred in both the control ($G = 34.571$, $df = 1$, $p < 0.001$) and post-cut sites ($G = 71.150$, $df = 1$, $p < 0.001$) and on shrub nests in the control sites ($G = 13.523$, $df = 1$, $p < 0.001$) in 1994, suggesting a significant year effect rather than a treatment effect.

Table 2-1. Mann-Whitney U statistics comparing predation rates of ground and shrub nests in 1993 and 1994, for all predators combined. Mean values are based on predation rates per cutblock or control block ($N_{\text{control}} = 10$ blocks, $N_{\text{treatment}} = 11$ cutblocks).

Site	Year	Mean Predation Rate		U	<i>p</i>
		Ground ($\pm$ S.E)	Shrub ($\pm$ S.E.)		
Control	1993	0.562 (0.057)	0.164 (0.047)	6	<0.001
Control	1994	0.849 (0.059)	0.445 (0.100)	13	0.002
Pre-cut	1993	0.298 (0.053)	0.307 (0.082)	51	0.859
Post-cut	1994	0.830 (0.046)	0.342 (0.043)	2	<0.001

Predator Identification

Three species of egg predators were identified from pictures taken by cameras placed at nests. One Blue Jay and 5 Red Squirrels were photographed at shrub nests; 2 Red-backed Voles and 1 Red Squirrel were photographed at ground nests. Identification of Red Squirrels as egg predators was corroborated by teeth marks in the plasticine eggs. Other teeth marks in plasticine eggs were attributed to Red-backed Voles or Deer Mice and unidentified mammals. Scratch marks on quail eggs were also attributed to Deer Mice or Red-backed Voles. There were also two incidental sightings of American Crows with eggs from unidentified bird species in their beaks (C. Burgess and I. Schmeltzer, pers. comm.).

Ground nests were primarily depredated by Deer Mice or Red-backed Voles (Table 2-2). These two species could not be separated by teeth imprints in the plasticine eggs. Cases of Deer Mouse/Red-backed Vole predation will be referred to as mouse predation events. The main identified shrub egg predator was the Red Squirrel. Avian predation events accounted for only a small proportion of all predation events. There were however, many instances where the predator at a shrub nest was not identified. Both eggs were taken from the nests in most of these cases. The primary suspected predators in these cases are Red Squirrels and Gray Jays. These assumptions are based on: 1) the low abundance of all corvids except Gray Jays and the high abundance of Red Squirrels in the study area (pers. obs.; F. Schmiegelow, pers. comm.); 2) incidental observations of songbirds mobbing Gray Jays (pers. obs.) and Gray Jays observed carrying a White-throated Sparrow (*Zonotrichia albicollis*) nestling (S. Diggon, pers.

Table 2-2. Proportion of predation events on ground and shrub nests attributed to major predator types. Proportions are based on the total number of ground and shrub nests depredated during 1993 and 1994 combined ($N_{\text{ground}} = 326$, $N_{\text{shrub}} = 164$).

Predator	% of all Predation Events	
	Ground	Shrub
Mouse	74	11
Red Squirrel	8	44
Avian	<1	4
Unidentified Mammal	2	2
Unidentified	15	39

comm.) and an American Redstart (*Setophaga ruticilla*) nestling (R. Robichaud, pers. comm.); 3) both eggs were damaged or removed in 99% of known squirrel predation events, compared to 25% of known mouse predation events; and 4) both Gray Jays and Red Squirrels are large enough to pick up an egg and remove it from a nest.

Plasticine Eggs

Two-thirds of the ground nests and approximately one third of the shrub nests that were depredated suffered partial losses where only one egg was damaged or missing. The scent of plasticine eggs may attract or repel potential egg predators or attract animals which are not usually egg predators. If there was no difference between the attractiveness of a quail egg and a plasticine egg to a predator, one would predict that in nests where only one egg was taken, 50% of those eggs would be plasticine and 50% would be quail. During the two years of the study, 268 nests had one egg removed; 235 of those eggs were plasticine and 33 were quail eggs. This is a significant departure from a 50:50 ratio (binomial test, $Z = 0.688$, $p < 0.001$).

Adjacency Effects

Larsen and Boutin (1994) reported that the average Red Squirrel territory size in a conifer dominated area was 0.65 ha (diameter = 90 m); mean territory size in a deciduous dominated area may be even larger because of more widespread resources. It is possible then, that 3 or 4 artificial nests could fall within a Red Squirrel territory. Red Squirrel predation events on shrub nests were tested for independence by comparing number of

observed with number of expected predation events. Expected number of nests depredated by Red Squirrels was determined using a two-sample binomial equation, $p^2 + 2pq + q^2$ (Sokal and Rohlf, 1981). The probability of occurrence was based on the average rate of predation of shrub nests, 13.4% ($N_{\text{red squirrel}} = 73$, $N_{\text{total}} = 544$), by Red Squirrels over the two year study. Therefore, the proportion of shrub nests depredated was $(p) = 0.134$ and the proportion nests not depredated was $(q) = 0.866$. Occurrence and independence of predation events were examined for two nests on either side of a 'central' nest that was depredated. The following possibilities were examined: 1) a central depredated nest having 2 adjacent nests depredated; the probability of occurrence of two predation events is $(p^2) = (0.134)^2 = 0.018$; 2) a central depredated nests having 1 adjacent nest depredated; the probability of occurrence of one predation event is $(2pq) = 2(0.134)(0.866) = 0.232$; 3) a central depredated nest having no adjacent nests depredated; the probability of occurrence of no adjacent nests depredated is $(q^2) = (0.866)^2 = 0.750$.

First and last nests on a transect were excluded because they could only be adjacent to one other nest. Red Squirrel predation events were significantly more clumped than expected, indicating a strong adjacency effect (Table 2-3). Clumping of Red Squirrel predation events occurred in control sites and fragmented treatment sites in 1994. Mouse predation events were not tested for independence because the events were common throughout the study sites and also because a mouse's home range would encompass only 1 or 2 nests.

Table 2-3. Observed and expected frequency of Red Squirrel predation events on shrub nests adjacent to depredated shrub nests compared to an expected random distribution, using a G-test. (N = 57).

Adjacency	Probability of Occurrence	Expected # of Nests		Observed # of Nests		G	df	p
		Depredated		Depredated				
2 adjacent nests depredated (p^2)	0.018	1.03		17		35.183	2	<0.001
1 adjacent nest depredated ($2pq$)	0.232	13.22		25				
0 adjacent nests depredated (q^2)	0.750	42.75		15				

Corvid Abundance and Species Composition

Four corvid species were identified from line-transect surveys: Gray Jay, Blue Jay, American Crow and Common Raven (Table 2-4). Common Raven and American Crow densities were not calculated because these species have large territories (e.g. Common Raven territory = 939 ha (Shank, 1986)) compared to the 22 ha to 30 ha covered by each transect survey. Additionally, many of the Common Raven and American Crow sightings were of individuals flying over the forest, not within the forest.

Blue Jays and American Crows were rarely observed within the study area. The Gray Jay was the most commonly observed corvid in pre-cut (1993), post-cut (1994) and control sites in 1994. The Common Raven was the most frequently sighted corvid in control sites in 1993. Number of Gray Jay sightings increased in 1994 in both control and post-cut sites, however these increases did not translate into significantly different densities when compared to 1993 densities (Wilcoxon Matched-Pairs Signed-Ranks test, $Z = -1.363$, $p = 0.173$, control sites; $Z = -0.765$, $p = 0.445$, pre- and post-cut sites). Blue Jay density and abundance appeared to decrease in 1994, particularly in the fragmented sites, however the densities were too low to test for significance.

Effect of Clearcutting on Egg Predation

Egg predation by mice and Red Squirrels increased significantly in both the control and fragmented sites in 1994, respectively (Table 2-5). No effect of clearcutting was apparent. No significant differences in predation rates were detected when comparing between control and pre-cut sites (1993), for all predators combined and for

Table 2-4. Number of Common Raven and American Crow sightings and densities of Gray Jay and Blue Jay recorded within control and fragmented sites in 1993 and 1994. Nine control transects and ten treatment transects were surveyed three times for 2 hours each visit during 1993 and 1994.

Sites	Range of Sightings/km of Transect				Range of Densities/ha [‡]			
	Common Raven		American Crow		Gray Jay		Blue Jay	
	1993	1994	1993	1994	1993	1994	1993	1994
Control								
Total # of Sightings	0-4 11	0-3 4	0-1 1	0-4 8	0-0.158 6	0-1.250 16	0-0.093 2	0-0.003 1
Fragmented*								
Total # of Sightings	0-2 12	0-3 10	0-1 2	0 0	0-0.763 19	0-2.663 33	0-0.291 10	0 3

[‡] Blue Jay and Gray Jay densities were determined from a full distance recording, line-transect method (Bibby *et al.*, 1992).

*Fragmented in 1994, 1993=Pre-cut

Table 2-5. Wilcoxon Matched-Pairs Signed-Ranks one-tailed test statistics comparing predation pressure between 1993 and 1994, within control and treatment sites. Predation events are grouped by predator type. Mean values are based on predation rates per cutblock or control block ($N_{\text{control}} = 10$ blocks, $N_{\text{treatment}} = 11$ cutblocks), power was determined using Cohen (1969).

Site	Predator	Mean Predation Rates			Z	p	Power
		1993 ($\pm$ S.E.)	1994 ($\pm$ S.E.)				
Control	All	0.330 (0.022)	0.639 (0.065)	-2.599	0.005	0.50	$P < 0.67$
Control	Mouse	0.182 (0.023)	0.330 (0.030)	-2.803	0.003	>0.86	
Control	Red Squirrel	0.052 (0.035)	0.202 (0.072)	-2.073	0.019	0.67	$P < 0.79$
Treatment	All	0.302 (0.051)	0.585 (0.032)	-2.756	0.003	0.70	
Treatment	Mouse	0.123 (0.037)	0.370 (0.027)	-2.845	0.002	0.82	
Treatment	Red Squirrel	0.016 (0.009)	0.128 (0.050)	-2.073	0.019	>0.89	

Red Squirrels (Table 2-6). There was a significant difference between mouse predation rates in control and pre-cut sites. This may indicate a site effect relating to vegetation or differences in mouse abundance. There were no differences in predation rates between control and post-cut sites for predation caused by all predators combined, mice or Red Squirrels.

Edge Effect

The effect of distance from a clearcut edge on the predation rate was examined using goodness of fit, maximum log-likelihood tests (G-tests). Nests were grouped into 13 distance classes; the first 7 distance classes were grouped in 20 m increments from a clearcut edge. Distance increments were pooled at distances greater than 120 m to increase sample sizes: 130-160 m, 180-240 m, 260-320 m, 340-400 m, 420-500 m and 520-680 m. Sample size ranged from 10-42 nests per distance class. Predation pressure remained constant regardless of distance from a clearcut edge. No relationships were found between distance from a clearcut edge and nest type or predator type (Table 2-7; Figure 2-4).

Vegetation Association

The influence of surrounding vegetation on nest success was examined separately for mouse predation events and Red Squirrel predation events in both 1993 and 1994. Increased lateral cover at the nest increased the probability of a nest being depredated by a mouse (Table 2-8). Overhead cover and canopy cover contributed moderately to the fit

Table 2-6. Mann-Whitney U one-tailed test statistics comparing predation rates between control and pre-cut sites and control and post-cut sites. Predation events are grouped by predator type. Power was determined using Cohen (1969) and a sample size of N = 10 blocks/treatment. Cont. = Control.

Comparison	Predator	Mean Predation Rates			U	p	Power
		Control ($\pm$ S.E.)	Treatment ($\pm$ S.E.)				
Cont. vs Pre-cut 1993	All	0.330 (0.022)	0.302 (0.051)	41	0.175	>0.86	
	Mouse	0.182 (0.023)	0.123 (0.037)	30	0.042	>0.86	
	Red Squirrel	0.052 (0.035)	0.016 (0.009)	52	0.432	>0.86	
Cont. vs Post-cut 1994	All	0.639 (0.065)	0.585 (0.032)	45.5	0.256	0.79<P<0.86	
	Mouse	0.330 (0.030)	0.370 (0.027)	39	0.141	>0.86	
	Red Squirrel	0.202 (0.072)	0.128 (0.050)	49.5	0.352	0.67	

Table 2-7. Effect of distance from a clearcut edge on egg predation rates in adjacent forest. G-tests were used to compare predation rates at 13 distance classes (0 to 680 m) from a clearcut edge. Predators and nest types were combined, and examined separately.

Nest Type	Number of Nests	Predator	G	df	p
Ground + Shrub	367	All predators	5.414	12	0.943
Ground + Shrub	367	Mouse	7.326	12	0.835
Ground + Shrub	367	Red Squirrel	9.317	12	0.676
Ground	185	All predators	9.886	12	0.626
Ground	185	Mouse	7.698	12	0.808
Shrub	182	All predators	9.297	12	0.677
Shrub	182	Red Squirrel	8.855	12	0.715

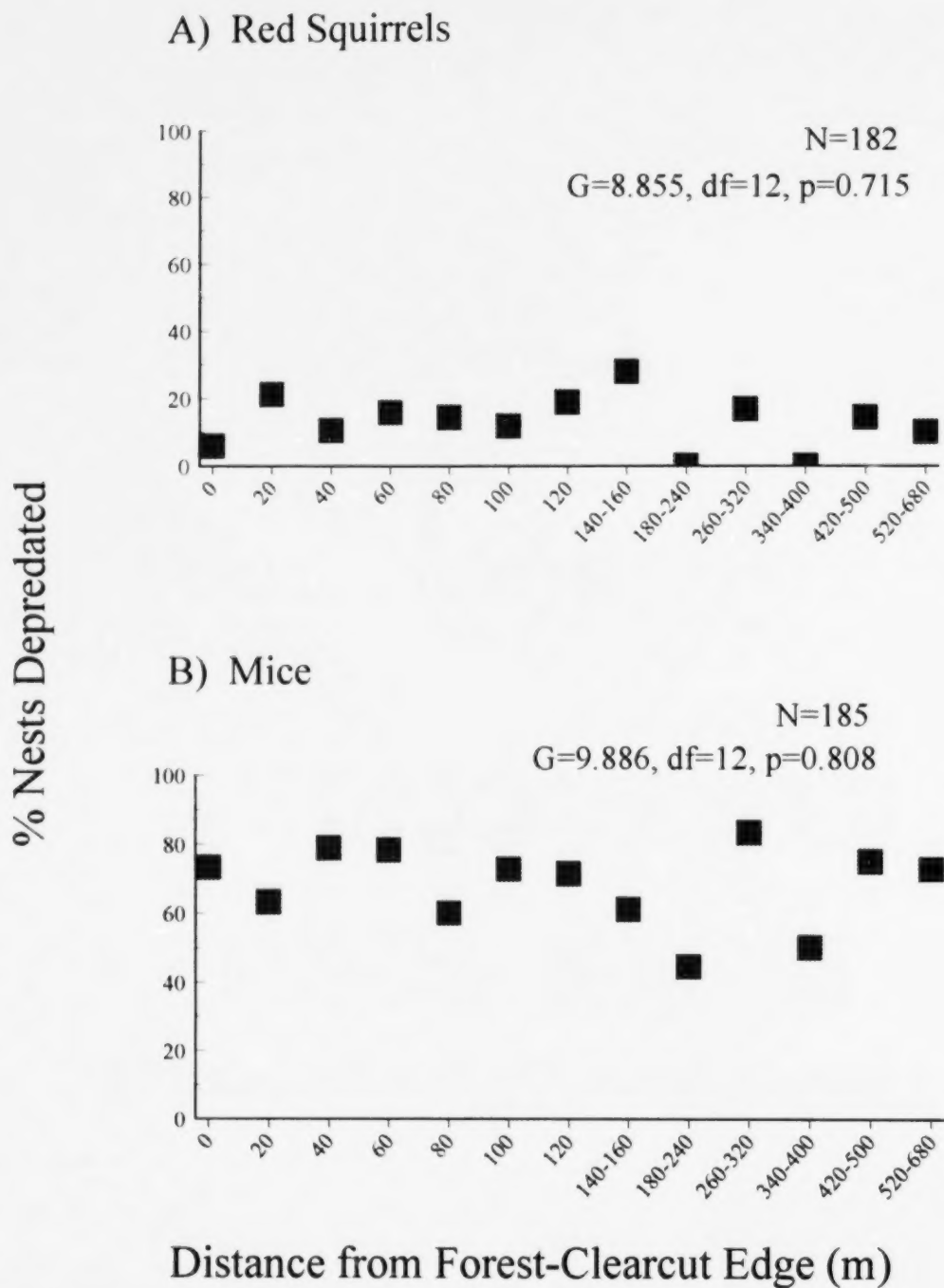


Figure 2-4. Percent of (A) shrub nests depredated by Red Squirrels and (B) ground nests depredated by mice, 0-680 m from forest-clearcut edge. Predation rates were not affected by distance from the edge (Red Squirrels, $G = 8.855$, $df = 12$, $p = 0.715$; mice, $G = 9.886$, $df = 12$, $p = 0.808$).

Table 2-8. Logistic regression models describing the influence of nest site vegetation characteristics on the probability of egg predation by mice. Predation was examined on a per nest basis. Nests were pooled for 1993 control and pre-cut sites and for 1994 control, post-cut and edge sites. Model improvement by each variable is expressed as a Chi-squared value and associated probability level.

Year	Nest Type	N	Model	Model Improvement		
				Variable	X ²	p
1993	Ground + Shrub	509	- 3.432 + (2.451 × LC)	LC	47.065	<0.001
1993	Ground	236	- 1.880 + (1.128 × LC)	LC	4.837	0.028
1994	Ground + Shrub	629	- 3.682 + (0.883 × OC) + (1.138 × CANC) + (1.926 × LC)	OC	14.482	<0.001
				CANC	5.387	0.020
				LC	66.595	<0.001
1994	Ground	319	No Significant Variables			

CANC = % Canopy Cover

LC = % Lateral cover at nest

OC = % Overhead cover at nest

of the 1994 ground and shrub nest model and increases of both of these variables elevated the probability of a nest being depredated by a mouse. However, despite the significance of the variables in contributing to the fit of the model, all of the models were very poor predictors of depredated nests. The models correctly classified 0% - 35% of depredated nests; between 83% and 100% of intact nests were classified correctly.

Percent herb cover, was consistently present as a parameter in Red Squirrel models (Table 2-9). Increasing herb cover was associated with a decreased probability of egg predation by Red Squirrels and significantly contributed to the fit of the model. Lateral cover at the nest and presence of a conifer tree as the dominant tree at the nest site decreased the probability of a nest being depredated by Red Squirrels. However, as with the mouse models, the Red Squirrel nest site vegetation models were extremely poor predictors of depredated nests. Only 0% - 7% of nests depredated by Red Squirrels were correctly classified by these models. In contrast, all nests not taken by Red Squirrels were correctly classified.

Landscape Context

Increasing length of seismic lines within a block was negatively associated with the probability of egg predation by mice in 1993 (Table 2-10). In 1994, however, increasing length of seismic lines, at all landscape scales was associated with an increased probability of egg predation by mice. Increasing area of bog or wetland and increasing deciduous and coniferous cover decreased the probability of egg predation by mice. All of these parameters were only moderate to weak contributors to the fit of the

Table 2-9. Logistic regression models describing the influence of nest site vegetation characteristics on the probability of egg predation by Red Squirrels. Predation was examined on a per nest basis. Nests were pooled for 1993 control and pre-cut sites and for 1994 control, post-cut and edge sites. Model improvement by each variable is expressed as a Chi-squared value and associated probability level.

Year	Nest Type	N	Model	Model Improvement		
				Variable	X ²	p
1993	Ground + Shrub	509	- 1.884 - (3.164 × HC)	HC	10.703	0.001
1993	Shrub	273	- 1.231 - (4.674 × HC)	HC	12.068	<0.001
1994	Ground + Shrub	629	- 0.690 - (1.190 × LC) - (0.794 × CON)	LC	11.884	0.001
				CON	9.887	0.002
1994	Shrub	310	- (-1.213 × HC) - (0.794 × CON)	HC	4.115	0.043
				CON	8.418	0.004

CON = Dominant tree at nest site is a Conifer

HC = % Herb cover

LC = % Lateral cover at nest

Table 2-10. Logistic regression models describing the influence of cutblock/block and landscape characteristics on the probability of predation of ground nests by mice. Mean predation rates were combined for control and pre-cut sites (1993) and control and post-cut sites (1994). Model improvement by each variable is expressed as a Chi-squared value and associated probability level. Only significant models are included.

Scale	Year	Model	Model Improvement		
			Variable	X ²	p
Block	1993	$-0.816 \times \text{SEIS}$	SEIS	10.444	0.001
Block	1994	$-(4.495 \times \text{CC}) + (6.747 \times \text{SEIS})$	CC	4.372	0.037
			SEIS	7.798	0.005
250 m + Block	1994	$0.964 - (5.782 \times \text{CC}) [250 \text{ m}] + (0.767 \times \text{SEIS}) [\text{block}]$ $-(1.266 \times \text{DC}) [250 \text{ m}]$	CC	6.708	0.010
			SEIS	7.705	0.006
			DC	5.351	0.021
450 m + Block	1994	$2.203 + (0.695 \times \text{SEIS}) [450 \text{ m}] - (4.059 \times \text{CC}) [450 \text{ m}]$ $-(1.768 \times \text{DC}) [450 \text{ m}]$	SEIS	8.916	0.003
			CC	9.754	0.002
			DC	4.842	0.028
1 km + Block	1994	$0.761 - (5.049 \times \text{CC}) [\text{block}] + (0.782 \times \text{SEIS}) [\text{block}]$ $-(3.882 \times \text{BW}) [1 \text{ km}]$	CC	5.386	0.020
			SEIS	8.123	0.004
			BW	4.720	0.030

BW = % Bog/Wetland Cover
 CC = % Conifer cover
 DC = % Deciduous cover
 SEIS = Length of seismic lines

model. The 1993 block attribute model was a very poor predictor of nests depredated by mice (0%), but an excellent predictor of nests not taken by mice (100%). The opposite was true for 1994 models; the majority of depredated nests (92%-100%) was correctly classified, while only a small proportion of intact nests was correctly classified (0%-18%).

Increasing amount of conifer cover and area covered by lakes or rivers were consistently associated with an increased probability of egg predation by Red Squirrels (Table 2-11). Increased deciduous cover at the 450 m and 1 km scales were also positively associated with egg predation by Red Squirrels. Increases in many landscape features including area of bog/wetland and 13 year old clearcut, length of seismic lines, width of block and presence of a natural open area within the block, were negatively related to the probability of egg predation by Red Squirrels. All of these model parameters significantly contributed to the fit of the model. However, the models were again, poor predictors. In 1993 no depredated nests were classified correctly, while all nests not taken by Red Squirrels were correctly classified. The 1994 models correctly classified 40% - 48% of depredated nests and 95% - 98% of nests not depredated.

Significance of the model parameters is one measure of the adequacy of the fit of a model. However, of more importance is the predictive capability of the model. The failure of the nest site vegetation and landscape features models to classify correctly depredated and intact nests indicates that models may be of little interpretive value. Only nest site and landscape level features, such as lateral cover, herb cover and percent

Table 2-11. Logistic regression models describing the influence of block and landscape characteristics on the probability of predation of shrub nests by Red Squirrels. Mean predation rates/block were combined for control and pre-cut sites (1993) and control and post-cut sites (1994). Model improvement by each variable is expressed as a Chi-squared value and associated probability level. Only significant models are included.

BW = % Bog/Wetland Cover	LR = % Lake or river cover	SEIS = Length of seismic lines
CC = % Conifer cover	NO = 0.45 ha natural opening in block	W = Width of block
DC = % Deciduous cover	OCC = % 13 year old clearcut cover	

Scale	Year	Model	Model Improvement		
			Variable	X ²	p
Block	1993	- 3.640 + (7.470 × CC)	CC	7.063	0.008
250 m + Block	1993	- 4.014 + (5.031 × CC) [250 m] - (40.511 × BW) [250 m]	CC BW	9.481 13.968	0.002 <0.001
450 m + Block	1993	- 23.889 + (25.429 × CC) [450 m] + (18.366 × DC) [450 m] + (25.696 × LR) [450 m]	CC DC LR	16.009 5.034 18.572	<0.001 0.025 <0.001
1 km + Block	1993	- 10.336 + (13.332 × CC) [1 km] + (12.448 × LR) [1 km]	CC LR	10.857 32.764	0.001 <0.001
Block	1994	- 7.990 + (16.297 × CC) - (1.359 × SEIS) - (1.280 × NO) - (18.675 × W)	CC SEIS NO W	25.110 13.073 41.777 29.565	<0.001 <0.001 <0.001 <0.001
1 km + Block	1994	- 19.1' + (14.283 × CC) [block] - (2.578 × NO) + (27.283 × CC) [1 km] + (17.013 × DC) [1 km] + (21.532 × OCC) [1 km] + (13.992 × LR) [1 km]	CC NO CC DC OCC LR	15.132 72.309 39.642 59.387 22.097 37.259	<0.001 <0.001 <0.001 <0.001 <0.001 <0.001

conifer content, that were consistently present in models and contributed significantly to the models may indicate an influence on egg predation by mice or Red Squirrels.

DISCUSSION

Effect of Forest Fragmentation by Clearcutting on Artificial Egg Predation

Elevated egg predation rates have often been associated with forest fragmentation and creation of edge (Gates and Gysel, 1978; Whitcomb *et al.*, 1981; Wilcove, 1985; Andr  n, 1992). However, I found no evidence to suggest an effect of clearcutting or the creation of edge on artificial egg predation rates. Predation rates increased in both the control and fragmented sites in 1994. The same trend was apparent in predation rates on American Redstart clutches (M-A. Villard and S. Hannon, unpub. data). The predation rates increased in 1994 compared to 1993 in control and fragmented sites within the study area (M-A. Villard and S. Hannon, unpub. data), suggesting a year effect. Gates and Gysel (1978) hypothesized that songbird densities would be greatest at edges due to abundant food, shelter and nest sites. In response to elevated songbird densities, egg predation should also increase at an edge. I observed a constant rate of predation on artificial nests, from a clearcut edge up to 680 m into continuous aspen mixedwood forest.

Yearly fluctuations in predator abundance can have a tremendous impact on egg predation rates (Maxson and Oring, 1978). Higher egg predation rates in control and fragmented sites in 1994 coincided with a three-fold increase in small rodent abundances in the study area from 1993-1994 (A. Chan-McLeod, unpub. data). In addition, an

abundant cone crop in 1993 (pers. obs.; F. Schmiegelow, pers. comm.) may have positively affected the overwinter survival and reproductive success of Red Squirrels. Fur trapping records for a 400 km² area which included my study area also suggest an increase in Red Squirrel populations in 1994. During the 1992-1993 trapping season, 780 Red Squirrels were trapped on 5 traplines in this area, while 1900 animals were trapped in the same area on 4 traplines during the 1993-1994 season (B. Treichel, pers. comm.). This strong year effect may have masked an increase in egg predation caused by fragmenting the landscape.

Presence of an edge-related increase in egg predation depends greatly on the species of predators, their densities and habitat use. In this study, ground nests were most commonly depredated by Deer Mice or Red-backed Voles. Previous studies have identified various species of mice as artificial egg predators (Ratti and Reese, 1988; Santos and Tellaria, 1992; Nour *et al.*, 1993; Leimbgruber *et al.*, 1994) and several *Peromyscus* species as predators of: Spotted Sandpiper (*Actitis macularia*) (Maxson and Oring, 1978), Xantus' Murrelet (*Synthliboramphus hypoleucus*) (Murray *et al.*, 1983) and Prothonotary Warblers (*Protonotaria citrea*) (Guillory, 1987) nests. Deer Mice are omnivorous and are more likely to be egg predators than Red-backed Voles which are primarily herbivores or granivores (Burt and Grossenheider, 1980). Red Squirrels were the primary identified predator of shrub nests. Contrary to other artificial egg predation studies in boreal forests (Angelstam, 1986; Andrén, 1992; Hannon, 1993), corvids were not important egg predators and little egg predation by birds was recorded during this study. However, the importance of corvids, particularly Gray Jays, as egg predators may

have been underestimated because the predator was not identified for many of the depredated shrub nests.

In a review of 40 artificial and natural egg predation studies, Andrén (1995) proposed three hypotheses to explain elevated egg predation rates at edges. First, predators may be attracted to a greater density of prey items found at edges. Several studies have documented increased songbird abundances at edges (Gates and Gysel, 1978; Strelke and Dickson, 1980). Andrén (1995) suggested that predators may actively search for nests along highly productive habitat interfaces. This first explanation does not apply well to this system because neither Red Squirrels nor mice appear to be strongly attracted to edge. Red Squirrels can be found throughout habitat patches from patch interior to edge, but they do not preferentially congregate at edges (S. Boutin, pers comm.). Distribution and density of Red Squirrels depends heavily on the distribution of their primary food and cover resource - mature conifer trees. In addition, Red Squirrel predation events were significantly more clumped than expected. Adjacent depredated nests were probably located within a Red Squirrel territory. These 'hotspots' occurred in unfragmented control sites as well as fragmented treatment sites in 1994 and may reflect conifer tree distribution. Deer Mice were observed in aspen-dominated stands and at aspen-clearcut edge in Alberta's boreal mixedwood, but did not show a preference for edge over forest sites (R. Weaver, unpub. data). Diffendorfer *et al.* (1995) also observed Deer Mice in remnant patches and in adjacent disturbed habitat. Deer Mice are habitat generalists, able to use a wide variety of habitat types including edge, but are not edge specialists.

Secondly, predators might use edges as natural travel lanes and incidentally find nests. Elevated predation pressure in this scenario may reflect greater time spent along an edge by predators, rather than nest density. Deer Mice and Red Squirrels have been observed to move large distances off their home range or territory (King, 1968; Larsen and Boutin, 1994, respectively), although little is known about movement along forest-clearcut edges by these two species. As an attraction to edge is not apparent, travel along edges by these two species may not be pronounced, except by individuals with territories adjacent to edges. Corvids have been observed at edges and associated with increased egg predation rates along edges (Wilcove, 1985; Møller, 1987; Andrén, 1992). Corvids were not, however, major egg predators nor were they common within my study area.

Finally, Andrén (1995) suggested that egg predation may be elevated at edges if the egg predators are habitat generalists living in the surrounding matrix and penetrating into habitat patches. Within the Calling Lake study area, Deer Mice and Red Squirrels were primarily found within forested areas. A penetration effect along the forest-clearcut edge probably would not occur because the main predators are not concentrated in clearcuts. There may however, be a penetration effect along natural edges if Deer Mice or Red Squirrels from conifer-dominated patches move into adjacent aspen patches. Examination of egg predation and predator movement along and across natural edges may be important to understanding the dynamics of egg predation in the boreal mixedwood. Nour *et al.*, (1993) also did not observe an edge-related increase in artificial egg predation in oak-dominated forests in Belgium. The major predator in that study was

the Eurasian Red Squirrel (*Sciurus vulgaris*), a forest-dwelling species that has been shown to be sensitive to forest fragmentation (Celada *et al.*, 1994).

The boreal mixedwood forest in my study area is a forest dominated landscape, composed of a variety of stand types, sizes and ages. Andrén (1995) found that increased egg predation near edges rarely occurred in forest mosaics composed of mature forest, clearcuts and regenerating stands; however, edge-related increases in egg predation were associated with forests located in agriculturally fragmented landscapes. Presence of a negative edge effect in farmlands and absence of one in forest mosaics is probably related to productivity of the landscape and to the predator community. Agricultural areas can support large populations of generalist predators because of plentiful and varied food sources. Higher density of predators in the agricultural matrix may result in an increase in egg predation along the field-forest interface. Differences in productivity among patches may not be as pronounced in forested landscapes. Edge-related increases in predation may not occur because of less disparity between predator densities among patches. Additionally, agricultural areas usually support a different predator community, which, in Alberta, include: Blue Jay, domestic cat (*Felis domestica*), Raccoon (*Procyon lotor*), American Crow, Black-billed Magpie and Striped Skunk (*Mephitis mephitis*). Corvids were four times more abundant in an agricultural area at Meanook Biological Station, 100 km south of Calling Lake, (S. Hannon, pers. comm.). The predators living in farmland are often habitat generalists and cause an increase in egg predation by penetrating into habitat patches from surrounding farmland. One other difference is that fields are often permanent 'open' areas whereas clearcuts regenerate relatively quickly.

The transitory nature of clearcuts probably does not favour predator species associated with open areas (e.g. American crow, Blue Jay).

Little evidence for negative effects of forest fragmentation by clearcutting may also relate to the patchiness of the boreal mixedwood ecoregion. A historical natural disturbance regime of frequent fires, insect outbreaks and windthrows has resulted in a complex mosaic composed of multiple habitat and stand types of varying size and age. Variation in topography and soil types across the region add to the complexity. Natural edges are common and exist at several scales, from the internal patchiness of a tree-fall gap, to the often extensive edge between habitat types. Edge context also varies from abrupt edges, such as a riparian-forest interface to soft edges where one stand type gradually grades into another. The animals that inhabit this ecosystem have adapted to existing in a heterogeneous environment.

Noss (1991) suggested that edge effects are greater in homogeneous forests and not as prominent in forests with gaps and greater internal patchiness, like boreal mixedwood forests. Creation of edge in a homogeneous landscape may attract birds and other wildlife species, such as predators, potentially resulting in negative edge effects. Anthropogenic edges, such as forest-clearcut edges, may not be as attractive when abundant resources may be found at gaps and natural edges in patchy forests. A mistnetting study conducted in the Calling Lake research area found no difference in number of bird captures at forest-clearcut edge compared to forest interior. This suggests that bird activity had not increased at forest-clearcut edges (C. Machtans, *et al.*, in press). Lack of increased bird activity at forest-clearcut edges and egg predators that do not

appear to congregate at edges suggests that an edge-related increase in egg predation caused by clearcutting may not occur in the boreal mixedwood system.

Influence of Nest Site Vegetation on Probability of Predation

Vegetation characteristics at several scales, from the nest site to features at the landscape level can influence egg predation. However, I found no strong relationships between nest site vegetation and probability of a nest being depredated by a mouse or Red Squirrel. Although the nest site vegetation models and model parameters were significant, these models were poor predictors of depredated and intact nests. While the models did not predict predation events well, nest site vegetation characteristics that were consistently present in the models may indicate an influence on egg predation by mice or Red Squirrels. Lateral cover at the nest site and herb cover were present in all mouse and three of four Red Squirrel models, respectively. Increased lateral cover at a nest suggests a denser ground vegetation which may provide Deer Mice with greater protection and concealment from predators. Merriam (1990) found that the closely related white-footed mouse (*P. leucopus*) preferred corridors with overhead and ground level cover. Greater herb cover may restrict Red Squirrel movement resulting in a lower predation rate.

Seitz and Zegers (1993) found no correlation between egg predation and ground cover or shrub density. However, reduced predation has been observed for both artificial and natural nests with greater foliage cover (Martin, 1992). Leimgruber *et al.* (1994) recorded increased artificial nest success where foliage density and herbaceous ground cover were higher and log density, rock and soil cover were reduced. Greater spatial

heterogeneity was found to increase the search time, decrease the foraging efficiency and reduce the number of artificial nests found by Raccoons (Bowman and Harris, 1980). Because Red Squirrels and mice rely on both olfactory and visual cues while foraging, cover at the nest and surrounding vegetation may not be important unless it restricts movement. Had the primary egg predators been sight predators, such as corvids, nest site vegetation may have negatively influenced probability of predation.

Influence of Landscape Features on the Probability of Egg Predation

Presence and amount of clearcutting did not affect the probability of predation events by mice or Red Squirrels. This supports the conclusion that clearcutting did not affect artificial egg predation rates. Despite having parameters that significantly contributed to the fit of the models, all of the mouse and Red Squirrel models generated were typically poor predictors of whether or not a nest was depredated. The poor fit of the models may be a reflection of high natural variability, such as fluctuations in predator abundance (ie. year effect), in this system.

Variables consistently present in the models may however, influence egg predation by mice or Red Squirrels. Length of seismic lines in and around blocks was present in all of the mouse models. Reduced competition from trees and shrubs may have resulted in increased growth of grasses and forbs in seismic lines, resulting in good foraging areas for mice. Increased conifer cover and area covered by a lake or river were consistently correlated with an increased probability of Red Squirrel predation events. These attributes may represent essential food, cover and nesting resources or areas

(riparian edge) of potentially high resources for Red Squirrels. Inclusion of these features in the models probably indicates increased Red Squirrel and mouse abundances which may be reflected in egg predation rates.

Limitations of Experimental Design

Artificial vs Natural Nests

Artificial nests are commonly used to assess egg predation rates. They cannot however, mimic natural nests, and use of artificial nests as an experimental tool has been questioned (Storaas, 1988; Willebrand and Marcström, 1988). Differences between artificial and natural nests may be caused by a variety of factors including: absence of adult bird activity on or near the nest, absence of nest defence by adult birds and lack of bird scent or the presence of human scent (Willebrand and Marcström, 1988; Yahner and Voytko, 1989). Placement, spacing, and concealment of nests by the researcher are probably very different from nest site selection by birds. Artificial egg experiments may not accurately estimate natural predation rates, but can be used as an index to compare predation rates between habitats or sites (Roper, 1992; Seitz and Zegers, 1993). Although predation rates were 10% - 20% higher on artificial nests, both the artificial shrub nests and American Redstart clutches within the study area experienced greater predation rates in control and fragmented sites in 1994 compared to 1993 (M-A. Villard, S.J. Hannon, unpub. data).

Significantly more plasticine eggs were removed or damaged in nests than quail eggs in this study. Red Squirrels and mice rely heavily on olfactory cues, and it is

possible that these animals were attracted to the scent of the artificial nests. While this attraction would have been an artifact of the experiment, it would have been constant across sites and between years. This finding suggests either an attraction to plasticine or the ability to more easily damage and mark the malleable plasticine.

Experimental Time Frame

This study was conducted over two years and included one pre-cut and one post-cut season. Immediate effects of clearcutting were not documented and may have been masked by a strong year effect in 1994, caused by fluctuations in predator abundance. Two or more post-cut seasons may have been necessary to account for the natural variation in the system. Additionally, long-term effects of clearcutting may become apparent after the second pass of harvesting has removed the majority of old aspen stands from the landscape.

Conclusions and Management Recommendations

I did not find any evidence of increased egg predation or changes to corvid abundances and species complex after clearcutting had occurred. The power of this study to detect differences in egg predation due to clearcutting was high. I would however caution that this was a one year post-cut study. Because of the tremendous increase in small mammal and Red Squirrel abundance in 1994, I recommend a longer-term study examining egg predation. A multi-year study would be substantially more robust to yearly fluctuations in predator abundance. Artificial egg predation studies

provide indirect measures of nest success, so ideally a multi-year study in this system would examine the effects of clearcutting on natural nests.

The next crucial step towards understanding the mechanisms which affect egg predation in the boreal mixedwood is to focus on the response of the primary egg predators to changes in landscape structure. Examination of Red Squirrel and Deer Mouse use of habitat and edge (natural and anthropogenic) at a regional scale may provide insight into the importance of the spatial context of landscape features and the processes that influence egg predation. Incorporation of spatial arrangement of patches, such as the configuration of aspen and conifer stands and riparian areas, into harvest planning may be important in terms of the ability of wildlife to move, disperse and survive in a fragmented landscape.

What may be of critical importance in the boreal mixedwood ecoregion is the overall loss of habitat and habitat heterogeneity which will occur. Despite the fragmentation in my study area, logging in the boreal mixedwood is in its infancy, and the landscape on a regional level is predominantly unfragmented by clearcuts. However, the large-scale and high intensity logging planned in the boreal mixedwood will result in widespread disruption of this ecosystem with a potential loss of biodiversity. I strongly encourage continued close monitoring of this ecosystem and the wildlife within as the pace of fragmentation accelerates.

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Appendix 1. Average canopy cover (CC), canopy height (CH), tree density (TDE), shrub density (SDE), herb cover (HC), herb height (HH), litter (LIT), lateral cover (LC) and overhead (OC) at nest sites, for control, treatment (pre-/ post-cut) and edge nest transects, used in logistic regression examining the influence of nest site vegetation on the probability of predation.

Transect	CC (%)	CH (m)	TDE (/m ²)	SDE (/m ²)	HC (%)	HH (m)	LIT (%)	LC (%)	OC (%)
Control									
c1n1	92.44	20.09	0.18	1.69	49.74	0.18	96.1	43.16	59.21
(± S.E.)	1.58	0.62	0.03	0.25	4.75	0.01	1.97	7.11	5.25
c1n2	89.87	21.95	0.17	2.45	47.35	0.23	98.8	39.41	63.82
(± S.E.)	1.92	0.42	200	0.43	5.66	0.02	0.53	6.30	6.87
c1n3	89.99	22.29	0.21	2.91	55.83	0.27	96.3	45.83	58.83
(± S.E.)	1.39	0.43	0.04	0.35	3.28	0.02	1.79	5.87	5.12
c1n4	91.23	22.04	0.15	2.32	52.00	0.23	92.8	46.75	56.50
(± S.E.)	0.94	0.58	0.04	0.42	4.51	0.02	2.22	6.69	6.90
c1n5	92.41	20.79	0.19	3.13	46.67	0.19	95.69	56.11	64.58
(± S.E.)	0.77	0.27	0.02	0.79	3.69	0.01	0.98	4.25	4.42
c2n1	91.97	20.40	0.18	3.36	54.60	0.24	94.40	42.40	57.40
(± S.E.)	1.24	0.37	0.02	0.72	4.24	0.02	2.03	5.14	5.44
c2n2	89.45	21.89	0.15	2.73	59.17	0.22	95.42	50.00	61.46
(± S.E.)	2.63	0.30	0.02	0.63	4.86	0.02	2.37	6.43	5.40
c3n1	94.03	25.95	0.13	3.20	45.63	0.22	99.13	48.38	58.88
(± S.E.)	0.49	0.43	0.01	0.25	3.41	0.01	0.43	4.60	4.76
c3n2	89.51	26.52	0.09	3.61	47.08	0.27	99.44	48.33	62.22
(± S.E.)	1.55	0.44	0.01	0.40	2.98	0.02	0.39	4.87	4.74
c4n1	92.51	17.99	0.18	1.34	39.68	0.19	98.55	43.19	58.23
(± S.E.)	0.94	0.42	0.03	0.14	3.93	0.01	0.78	4.38	4.59
c4n2	91.04	21.29	0.11	2.45	47.89	0.25	97.37	48.68	74.74
(± S.E.)	1.22	0.80	0.02	0.48	0.43	0.02	1.89	5.83	4.58
c5n1	81.96	25.85	0.08	3.35	52.76	0.28	99.66	53.10	68.45
(± S.E.)	2.29	0.55	0.01	0.32	3.91	0.02	0.34	4.46	4.31
c5n2	83.83	23.68	0.11	3.05	43.13	0.27	99.53	40.63	64.33
(± S.E.)	2.05	0.67	0.02	0.39	3.83	0.02	0.34	5.07	4.86
c5n3	92.97	21.91	0.14	3.47	48.18	0.34	99.77	48.86	57.95
(± S.E.)	1.83	0.48	0.02	0.54	4.48	0.02	0.23	6.03	5.70

Appendix 1 continued.

Transect	CC (%)	CH (m)	TDE (/m ²)	SDE (/m ²)	HC (%)	HH (m)	LIT (%)	LC (%)	OC (%)
c6n1 (± S.E.)	94.05 0.85	20.25 0.38	0.15 0.02	1.95 0.29	41.88 4.70	0.22 0.02	92.29 4.15	42.29 4.81	71.67 4.44
c6n2 (± S.E.)	90.81 0.88	22.40 0.54	0.12 0.02	3.54 0.44	41.57 4.14	0.18 0.01	89.43 3.51	40.86 4.56	53.57 5.38
c7n2 (± S.E.)	86.93 1.05	23.77 0.35	0.08 0.01	3.71 0.48	50.00 4.51	0.18 0.01	93.89 2.66	53.93 7.43	67.86 9.03
c8n1 (± S.E.)	93.34 1.27	20.63 0.40	0.10 0.02	3.38 0.45	46.73 3.82	0.23 0.01	96.92 1.96	37.31 4.68	60.38 5.88
c8n2 (± S.E.)	91.49 1.08	22.75 0.32	0.07 0.01	3.19 0.30	54.85 3.67	0.25 0.01	97.94 2.06	37.35 4.41	58.09 5.13
Pre-/Post-Cut									
34482n1 (± S.E.)	80.55 2.97	23.55 0.53	0.09 0.01	3.45 0.47	49.38 4.05	0.30 0.02	99.38 0.46	56.67 6.31	67.92 5.73
34482n2 (± S.E.)	90.99 1.46	21.48 0.51	0.11 0.01	3.04 0.42	52.97 3.87	0.24 0.01	99.53 0.47	47.97 4.89	60.31 5.39
34972n1 (± S.E.)	82.64 2.36	22.83 0.49	0.08 0.01	2.40 0.51	45.56 4.28	0.23 0.02	98.52 1.16	45.19 4.87	62.41 5.03
34972n2 (± S.E.)	92.79 1.35	23.42 0.40	0.20 0.02	3.24 1.19	50.00 3.89	0.20 0.01	97.61 1.21	40.87 5.01	63.70 6.85
35482n1 (± S.E.)	84.58 2.27	18.33 0.39	0.16 0.02	1.30 0.34	45.91 4.65	0.18 0.02	81.59 4.45	55.23 6.64	58.86 5.60
35532n1 (± S.E.)	83.50 2.29	21.98 0.37	0.15 0.02	2.68 0.44	65.83 2.83	0.25 0.01	93.96 3.78	53.75 7.34	54.17 7.00
30682n1 (± S.E.)	82.54 1.71	22.26 0.41	0.14 0.02	6.19 0.78	50.17 4.51	0.22 0.02	99.48 0.52	55.0 4.88	70.17 4.94
30682n2 (± S.E.)	77.58 2.57	17.97 0.46	0.16 0.02	2.36 0.57	48.82 3.40	0.18 0.01	98.68 0.75	49.21 4.43	54.24 4.01
31322n1 (± S.E.)	87.01 1.98	25.08 0.37	0.13 0.02	5.47 0.73	54.00 4.99	0.25 0.02	98.00 1.05	52.75 7.32	63.75 6.58
31322n2 (± S.E.)	92.25 1.49	24.18 0.31	0.12 0.01	4.30 0.65	59.17 3.00	0.18 0.01	96.25 1.40	58.47 4.59	58.61 4.10

Appendix 1 continued.

Transect	CC (%)	CH (m)	TDE (/m ³)	SDE (/m ³)	HC (%)	HH (m)	LIT (%)	LC (%)	OC (%)
30942n1 (± S.E.)	90.76 2.47	21.05 0.51	0.13 0.02	2.42 0.58	51.13 3.85	0.19 0.01	96.77 1.40	55.48 4.69	67.74 4.13
30942n2 (± S.E.)	92.34 0.88	21.37 0.54	0.16 0.02	1.74 0.89	59.44 4.59	0.19 0.02	99.63 0.26	50.00 4.94	58.33 5.04
28722n1 (± S.E.)	90.02 1.51	22.40 0.41	0.16 0.03	2.32 0.37	55.00 4.19	0.18 0.02	94.79 1.96	58.96 5.43	62.92 5.63
28722n2 (± S.E.)	82.41 2.48	20.51 0.50	0.12 0.02	3.05 0.55	55.52 4.29	0.20 0.02	98.79 0.59	44.14 5.17	59.66 5.64
29492n1 (± S.E.)	89.11 1.25	21.65 0.47	0.15 0.01	3.45 0.53	50.30 4.75	0.23 0.01	99.24 0.62	51.36 3.16	58.79 5.25
29492n2 (± S.E.)	80.28 1.99	18.47 0.34	0.13 0.02	3.03 0.50	59.00 3.61	0.23 0.01	99.14 0.38	52.14 4.69	67.43 3.47
29182n1 (± S.E.)	88.25 1.63	20.85 0.51	0.21 0.05	3.19 0.72	56.48 5.20	0.23 0.02	99.07 0.93	48.89 5.28	63.33 5.04
29182n2 (± S.E.)	86.63 1.93	18.84 0.39	0.14 0.01	4.77 1.00	47.32 3.84	0.20 0.01	99.11 0.52	48.04 4.71	66.43 4.86
31942n1 (± S.E.)	92.61 1.61	22.18 0.55	0.14 0.03	4.58 0.59	63.75 4.20	0.23 0.01	99.00 0.58	69.5 4.31	72.75 3.78
Edge									
e1 (± S.E.)	88.89 0.89	23.47 0.31	0.16 0.02	2.89 0.22	57.50 2.60	0.31 0.01	95.97 2.06	45.40 3.32	66.37 3.40
e2 (± S.E.)	87.88 1.40	22.36 0.60	0.11 0.02	3.05 0.38	54.26 3.12	0.34 0.02	98.97 0.66	49.26 5.28	62.35 5.40

Appendix 2. Landscape attributes within control blocks and treatment cutblocks for 1993 and 1994, used in logistic regressions to determine the influence of landscape structure on the probability of nest predation.
Con. = Conifer, Can.=Canopy.

Block #	Area (ha)	Edge (km)	Width (km)	E:A	% Con. Content	% Can. Cover	Natural Opening	Old Clearcut	Seismic Line (km)
Control 1993									
1	-	-	-	-	15.0	90.0	No	No	1.04
2	-	-	-	-	31.0	91.3	No	No	0.94
3	-	-	-	-	7.5	91.9	No	No	0.60
4	-	-	-	-	0.1	90.9	No	No	0.40
5	-	-	-	-	1.3	94.4	No	No	0
6	-	-	-	-	1.9	94.2	Yes	Yes	1.10
7	-	-	-	-	2.4	83.9	Yes	No	0.40
8	-	-	-	-	0	96.1	No	Yes	0.50
9	-	-	-	-	20.8	92.1	No	No	0.28
10	-	-	-	-	12.5	87.1	No	No	1.96
11	-	-	-	-	4.8	91.3	No	No	1.00
Control 1994									
1	40.0	2.8	0.4	0.07	12.5	92.3	No	No	1.04
2	40.0	2.8	0.4	0.07	1.6	89.0	No	No	0.94
3	40.0	2.8	0.4	0.07	4.2	92.1	No	No	0.60
4	40.0	2.8	0.4	0.07	2.9	90.6	No	No	0.40
5	40.0	2.8	0.4	0.07	1.9	89.5	No	No	0
6	40.0	2.8	0.4	0.07	1.9	90.0	Yes	Yes	1.10
7	40.0	2.8	0.4	0.07	5.6	82.0	Yes	No	0.40
8	40.0	2.8	0.4	0.07	0	90.4	No	Yes	0.50
9	40.0	2.8	0.4	0.07	15.0	92.2	No	No	0.28
11	40.0	2.8	0.4	0.07	3.2	93.2	No	No	1.00
Pre-cut 1993									
1	-	-	-	-	5.8	89.9	No	No	1.88
2	-	-	-	-	12.5	88.9	No	No	1.22
3	-	-	-	-	20.5	88.4	Yes	No	0.56
4	-	-	-	-	0	92.2	Yes	No	0.08
5	-	-	-	-	2.9	84.3	Yes	No	2.22
6	-	-	-	-	8.9	88.6	No	No	0.22
7	-	-	-	-	29.2	93.3	No	No	0.98
8	-	-	-	-	4.6	89.0	No	No	1.38
9	-	-	-	-	2.1	87.8	Yes	No	0.64
10	-	-	-	-	0	92.3	Yes	No	0.30
11	-	-	-	-	0	3.2	No	No	1.14
Post-cut 1994									
1	22.6	2.557	0.240	0.113	6.3	85.8	No	No	1.14
2	29.0	3.909	0.308	0.135	16.1	87.7	No	No	1.22
3	19.0	2.355	0.254	0.124	15.9	84.6	Yes	No	0.56
4	17.0	2.429	0.257	0.143	0	83.5	Yes	No	0.08
5	27.0	2.948	0.338	0.109	5.0	80.1	Yes	No	1.28
6	28.0	3.537	0.286	0.126	8.0	89.6	No	No	0.22

Appendix 2 continued.

Block #	Area (ha)	Edge (km)	Width (km)	E:A	% Con Content	% Canopy Cover	Natural Opening	Old Clearcut	Seismic Line (km)
7	28.0	2.532	0.274	0.090	21.1	91.6	No	No	0.30
8	30.0	3.249	0.288	0.108	3.6	86.2	No	No	1.38
9	20.5	2.558	0.305	0.125	6.5	84.7	Yes	No	0.22
10	25.5	2.708	0.261	0.106	0	87.4	Yes	No	0
11	14.0	1.977	0.215	0.141	0	92.6	No	No	0.64

Appendix 3. Landscape attributes surrounding control blocks and treatment cutblocks within 250 m, 450 m and 1 km, used in logistic regressions to determine the influence of landscape structure on the probability of nest predation. Con.=Coniferous, Decid.=Deciduous, W.land=Wetland.

Block #	% Con.	% Decid.	%River /Lake	% Clearcut	% Old Clearcut	% Bog W.land	Seismic Line(km)
250 m							
Control 1993							
1	31.3	68.7	0	0	0	0	2.30
2	30.4	57.5	0	0	0	12.0	1.70
3	31.9	50.9	2.3	0	0	14.9	1.68
4	46.3	40.1	1.6	0	0	12.0	0.98
5	39.1	37.8	15.8	0	0	7.4	1.50
6	23.6	35.3	0	0	36.4	4.6	2.68
7	19.3	80.7	0	0	0	0	2.54
8	5.6	52.1	0	0	42.3	0	1.84
9	59.5	36.4	4.7	0	1.2	0	2.40
10	59.2	27.8	13.0	0	0	0	2.16
11	29.4	47.5	22.4	0	0.7	0	1.64
Control 1994							
1	31.3	68.7	0	0	0	0	2.30
2	30.4	57.5	0	0	0	12.0	1.70
3	31.9	50.9	2.3	0	0	14.9	1.68
4	46.3	40.1	1.6	0	0	12.0	0.98
5	39.1	27.4	15.8	10.3	0	7.4	1.50
6	23.6	35.3	0	0	36.4	4.6	2.68
7	19.3	80.7	0	0	0	0	2.54
8	5.6	52.1	0	0	42.3	0	1.84
9	59.5	36.4	4.7	0	1.2	0	2.40
11	29.4	47.5	22.4	0	0.7	0	1.64
Pre-cut 1993							
1	23.6	74.1	0	0	0	2.2	1.12
2	45.0	48.9	0	0	0	6.1	1.12
3	41.9	32.0	0	0	0	26.0	1.16
4	54.6	45.1	1.7	0	0	1.1	1.26
5	16.2	73.5	0	0	0	10.5	2.24
6	41.1	34.0	0	0	0	15.4	1.12
7	33.8	67.0	0	0	0	0	0.80
8	35.4	54.9	0	0	0	4.9	1.22
9	23.9	69.9	0	0	0	6.2	2.00
10	5.8	91.5	0	0	0	2.7	1.06
11	31.7	63.9	0	0	0	0	2.08
Post-cut 1994							
1	23.6	17.1	0	57.0	0	2.2	1.12
2	45.0	8.3	0	40.6	0	6.1	1.12
3	41.9	0.4	0	31.6	0	26.0	1.16
4	54.6	15.1	1.7	30.0	0	1.1	1.26

Appendix 3 continued.

Block #	% Con.	% Decid.	%River /Lake	% Clearcut	% Old Clearcut	% Bog W.land	Seismic Line(km)
5	16.2	15.9	0	57.6	0	10.5	2.24
6	41.1	9.4	0	33.6	0	15.4	1.12
7	33.8	9.4	0	57.6	0	0	0.80
8	35.4	16.8	0	38.1	0	4.9	1.22
9	23.9	12.0	0	57.9	0	6.2	2.00
10	5.8	22.5	0	69.0	0	0	1.06
11	31.7	22.3	0	41.6	0	0	2.08

450 m

Control 1993

1	36.6	63.4	0	0	0	0	5.30
2	28.8	55.7	0	0	0	12.1	3.12
3	29.2	47.8	2.5	0	0	20.3	4.04
4	44.1	38.1	0	0	0	17.0	1.82
5	28.8	38.5	29.4	0	0	3.5	3.40
6	24.1	36.7	0.5	0	35.6	3.0	7.52
7	27.8	72.2	0	0	0	0	5.41
8	17.4	41.5	0	0	40.2	0.8	4.52
9	50.9	31.5	17.9	0	0.6	0	3.62
10	48.6	33.9	17.1	0	0	0	5.26
11	21.2	47.3	31.2	0	0.3	0	5.30

Control 1994

1	36.6	63.4	0	0	0	0	5.30
2	28.8	55.7	0	0	0	12.1	3.12
3	29.2	47.8	2.5	0	0	20.3	4.04
4	44.1	38.1	0	0	0	17.0	1.82
5	28.8	31.8	29.4	2.2	0	3.5	3.40
6	24.1	36.7	0.5	0	35.6	3.0	7.52
7	27.8	72.2	0	0	0	0	5.41
8	17.4	41.5	0	0	40.2	0.8	4.52
9	50.9	31.5	17.9	0	0.6	0	3.62
11	21.2	45.3	31.2	2.0	0.3	0	5.30

Pre-cut 1993

1	35.5	59.6	0	0	0	16.0	4.34
2	38.8	58.2	0	0	0	0	2.12
3	42.0	30.3	1.3	0	0	26.4	3.40
4	49.0	45.0	2.0	0	0	5.1	2.74
5	23.5	64.1	0	0	0	11.9	4.56
6	39.8	40.7	5.6	0	2.9	11.5	4.84
7	28.0	70.6	0	0	0	1.3	2.30
8	47.6	41.6	0	0	0	6.3	3.23
9	30.0	65.4	0	0	0	5.0	4.26
10	13.2	83.4	0	0	0	3.4	4.16
11	31.8	62.9	0	0	0	0	5.04

Appendix 3 continued.

Block #	% Con.	% Decid.	%River /Lake	% Clearcut	% Old Clearcut	% Bog W.land	Seismic Line (km)
Post-cut 1994							
1	35.5	23.7	0	35.9	0	16.0	4.34
2	38.8	24.2	0	34.0	0	0	2.12
3	42.0	8.1	1.3	22.2	0	26.4	3.40
4	49.0	20.4	2.0	24.6	0	5.1	2.74
5	23.5	27.2	0	36.9	0	11.9	4.56
6	39.8	17.5	5.6	23.2	2.9	11.5	4.84
7	28.0	32.3	0	38.3	0	1.3	2.30
8	47.6	15.1	0	26.5	0	6.3	3.23
9	30.0	25.8	0	39.6	0	5.0	4.26
10	13.2	34.5	0	48.9	0	3.4	4.16
11	31.8	35.6	0	27.3	0	0	5.04
1 km							
Control 1993							
1	43.6	44.9	0.2	0	0	11.2	12.54
2	33.4	39.9	0.8	0	0	24.2	6.04
3	38.3	41.7	1.1	0	0	19.0	11.98
4	37.2	41.4	0.2	0	0	21.1	11.46
5	23.9	41.9	31.1	0	0	3.2	7.32
6	27.8	15.6	4.4	0	15.9	2.4	23.38
7	28.6	65.6	0	0	3.1	2.4	14.29
8	29.0	43.9	0	0	26.0	0.9	19.08
9	40.0	24.3	34.1	0	0.2	2.0	10.65
10	45.8	29.3	24.8	0	0	0	13.88
11	28.8	31.4	38.3	0	0.3	0.9	11.12
Control 1994							
1	43.6	44.9	0.2	0	0	11.2	12.54
2	33.4	39.9	0.8	0	0	24.2	6.04
3	38.3	41.7	1.1	0	0	1.9	11.98
4	37.2	41.4	0.2	0	0	21.1	11.46
5	22.4	36.9	31.1	4.4	0	3.2	7.32
6	27.8	15.6	4.4	0	15.9	2.4	23.38
7	25.5	57.2	0	11.7	3.1	2.4	14.29
8	29.0	43.9	0	0	26.0	0.9	19.08
9	40.0	23.7	34.1	0.2	0.2	2.0	10.65
11	32.9	27.1	38.3	5.0	0.3	0.9	11.12
Pre-cut 1993							
1	48.4	48.8	0.2	0	0	2.4	14.84
2	43.2	47.7	1.1	0	0	8.1	12.40
3	39.8	34.5	3.4	0	0	24.1	13.56
4	43.8	41.4	2.2	0	0	15.3	12.36
5	31.4	55.7	3.9	0	1.0	4.3	12.94

Appendix 3 continued.

Block #	% Con.	% Decid.	%River /Lake	% Clearcut	%Old Clearcut	% Bog W.land	Seismic Line(km)
6	41.0	37.0	11.3	0	5.1	5.6	8.38
7	29.8	63.0	5.9	0	0	1.3	9.80
8	50.9	38.4	4.2	0	0	6.5	11.19
9	32.1	60.3	3.6	0	0	4.0	16.34
10	35.7	63.8	0.5	33.2	0	1.8	18.56
11	38.0	53.3	5.2	0	0	3.6	14.34
Post-cut 1994							
1	48.4	25.8	0.2	23.0	0	2.4	14.84
2	43.2	26.3	1.1	21.4	0	8.1	12.40
3	39.8	14.9	3.4	19.6	0	24.1	13.56
4	43.8	20.4	2.2	21.0	0	15.3	12.36
5	31.4	27.6	3.9	28.1	1.0	4.3	12.94
6	41.0	18.3	11.3	18.7	5.1	5.6	8.3
7	29.8	43.2	5.9	19.8	0	1.3	9.80
8	50.9	19.0	4.2	19.4	0	6.5	11.19
9	32.1	33.5	3.6	26.8	0	4.0	16.34
10	35.7	30.6	0.5	33.2	0	1.8	18.56
11	38.0	30.8	5.2	22.5	0	3.6	14.34